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Does foliage on the same branch compete for the same water?
Experiments on Douglas-fir trees

Abstract Do branchlets within a branch have autonomous water supplies, or do they share a common water supply system? We hypothesized that if branchlets shared a common water supply, then stomatal conductance (g_s) on sunlit foliage would increase with reduced transpiration of competing foliage on the branch. We reduced transpiration of other foliage on the branch through bagging and shading, and we monitored the gas-exchange responses of the remaining sunlit foliage on the branch relative to control branches for several age classes of Douglas-fir trees (aged ~10 years, 20 years, and 450 years old). Contrary to our hypothesis, we found no increases in g_s in either young or old trees following transient reductions in the amount of transpiring leaf area. The diurnal change in water potential, mid-day stomatal closure and associated photosynthetic decline occurred at the same time and were of the same magnitude on both treated and untreated branches, with the exception of photosynthesis in one 450-year-old tree. Hydraulic conductance measurements of branch junctions indicate that xylem within branches is only partially interconnected which would reduce the effectiveness of shading as a means of increasing water supply to the remaining sunlit foliage. The lack of a response implies that when a branch is in partial shade, the remaining sunlit foliage has no advantage with respect to water status over foliage on a branch completely in the sun.

Keywords Leaf specific conductance · Sapwood area/leaf area ratio · Hydraulic conductance · Shading · Pseudotsuga menziesii

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Introduction

Stomatal conductance (g_s) is regulated by complex interactions including the supply of water to the leaf and the evaporative demand for water in the atmosphere (Jarvis and McNaughton 1986; Schulze 1986; Hinckley et al. 1991; Whitehead 1998). The supply of water to the leaf is controlled both by soil moisture and by the capacity of the tree to conduct water (Richter 1973), whereas the evaporative demand is largely driven by solar radiation and the vapor pressure deficit (Monteith 1965).

Many studies have shown a strong correlation between g_s and leaf specific conductance of the wood supplying water to the foliage (Meinzer and Grantz 1990; Meinzer et al. 1999; Ewers et al. 2000; Nardini and Salleo 2000; Hubbard et al. 2001). When evaporative demand is relatively constant, g_s varies directly with the leaf specific conductance of the supplying wood. Nardini and Salleo (2000) examined 11 different woody species growing in an arboretum, and found that variation in leaf specific hydraulic conductance of the shoot accounted for approximately 60% of the variation in maximum leaf conductance to water vapor. Manipulative experiments in which leaf specific conductance is altered either by reducing hydraulic conductance of the stem or altering leaf area show mixed results with respect to their effect on stomatal conductance. A reduction of g_s has been observed in many experiments that lower the hydraulic conductance of a stem (Teskey et al. 1985; Cernusak and Marshall 2001; Hubbard et al. 2001), but not always

(Hubbard et al. 1999). However, experimental reductions in leaf area either by shading or defoliation have had even more variable results. The expected result is that g_s would increase with reductions of total leaf area (Meinzer and Grantz 1990; Whitehead et al. 1996; Pataki et al. 1998; Hart et al. 2000), but in some cases g_s did not respond, or even decreased after partial leaf removal or shading. For example, when Whitehead et al. (1996) shaded only 22% of the upper crown of *Pinus radiata* (Monterey Pine), they did not find an increase in g_s in the remaining 78% of the lower canopy. However, they found a significant increase in g_s in the upper canopy foliage when they shaded the lower 78% of the canopy. Hubbard et al (1999) only saw transitory affects of partial defoliation of branches on g_s of the remaining foliage in old *Pinus ponderosa*, and they did not detect any response in young trees to this treatment. Syvertsen (1994) found no stomatal response to partial defoliation even though photosynthesis increased when leaf area was reduced in *Citrus* seedlings. Troeng and Langstrom (1991) found reductions in stomata conductance and photosynthesis after pruning a 20-year old *Pinus sylvestris* tree. Although a strong relationship exists between g_s and leaf specific conductance, alterations to that hydraulic system produce highly mixed results.

The interpretation of leaf-specific conductance measurements usually assume that all foliage downstream functions equally, and all leaves have equal access to the water, because the measurement of conductance is divided by total leaf area. However, since shading reduces transpiration, "realized" leaf specific hydraulic conductance would vary with the amount of leaf area that is transpiring at any one time. Not every unit of foliage is equally exposed to the driving forces for transpiration, and as a consequence, transpiring leaf area is less than total leaf area of a tree (Cermak 1989; Cermak et al, unpublished data). Considerable variation in the diurnal pattern of transpiration can be attributed to the degree of foliar illumination (Wang and Jarvis 1990). Martin et al. (2001) found that diurnal variation in radiation exposure explained most of the temporal variation in branch transpiration in old growth *Abies amabilis*. If shading one part of a branch does alter the effective leaf-specific hydraulic conductance of a branch, then one would expect that sunlit foliage on a partially shaded branch would have higher g_s than sunlit foliage on a fully illuminated branch.

Our objectives in this study were to determine if reductions in transpiring leaf area through shading would increase g_s for the remaining sunlit foliage of a branch. We selected the branch as an experimental unit, because for short-term manipulations they can be treated as relatively autonomous units (Sprugel et al. 1991), and because of their suitability as an intermediate scale between leaves and whole trees (Teskey et al. 1991; Hinckley et al. 1998). We compared stomatal response to reductions in transpiring leaf area of branches in *Pseudotsuga menziesii* trees covering a range of ages to determine the robustness of our results. Finally, we tested whether branches were hydraulically interconnected such that shading in one portion of a branch could increase water supply for the remaining sunlit portions.

Materials and methods

Study site

Seven trees in three separate stands of *Pseudotsuga menziesii* (Douglas-fir) were selected to address the above objectives: four trees in a 10-year-old cluster of trees, two trees in a 20-year-old stand, and one tree in a 450-year-old stand. The 10-year-old trees were located at the EPA campus at Corvallis, Oregon (44°34′ N, 123°17′W, 70 m a.s.l.). The other two stands were located within the Wind River Experimental Forest in southwestern Washington (45°49′N, 121°57′W). The low sample size in the Wind River stands was due to constraints on canopy access to sun-exposed branches. The 450-year-old stand was located at the Wind River Canopy Crane Research Facility within the T.T. Munger Research Natural Area at 368-m elevation, whereas the 20-year-old stand was located 3.7 km west at 558 m.

The climate of the two areas is typical of a temperate coastal climate, with mild wet winters and dry summers. For the Wind River stands, annual precipitation is approximately 2,500 mm of which less than 10% occurs between June and September; average annual snowfall is 2,330 mm, and mean annual temperature is 8.7°C (data from Wind River Ranger Station). In Corvallis, annual precipitation is lower than at Wind River, approximately 1,100 mm with a similar seasonal pattern, but average annual snowfall is 200 mm. Mean annual temperature in Corvallis is 11°C (data from the Oregon Climate Service, Corvallis Station).

Experimental design

We used a paired-branch experimental design to address our objectives. Two sun-exposed branches were selected on each of the seven experimental trees; one branch of each pair was randomly selected for treatment, while the other served as a control. For the young trees (10- and 20-year-olds), branches on the same whorl were selected for similarity in exposure, leader length and branch diameter. On the old tree, two exposed, large branches in the upper crown (between 55 and 60 m) were selected for similarity in size and crane accessibility.

The treatment consisted of bagging and shading 85–90% of the foliage on the treatment branch and monitoring the gas exchange and twig water potential of the remaining sunlit foliage as well as total xylem water fluxes in that branch. At the same time, we monitored xylem water flux, gas exchange and water potential of similar sunlit foliage on the control branch throughout a day. Baseline differences between the branch pairs were measured prior to bagging and shading by monitoring all branches for xylem water flux, gas exchange and water potential over a day. After the pretreatment diurnal measurements were complete, the treatment branches were shaded by loosely enclosing the foliated parts inside white plastic drawstring bags, and then placing aluminum foil over the plastic bags. Selected foliated shoots on the treatment branches remained uncovered for gas exchange and water potential measurements the following day. Each treatment branch was shaded for at least 15 h prior to a repeat set of diurnal measurements that included sap flux, gas exchange and water potential.

Measurement techniques

Gas exchange was measured on 1-year-old, fully sunlit foliage using a portable photosynthesis system (LI-6400, LI COR, Lincoln, Neb., USA) with a red-blue light source (6400–02B). For each branch on each of the 2 measurement days, two or three foliage samples per branch were repeatedly measured between 0700 and

1600 hours. All gas-exchange measurements were made at light saturation (1,500 µmol m^{-2} s^{-1}) with CO_2 concentrations of the reference gas at 400 ppm. After the diurnal measurements were completed, foliage samples were collected and projected leaf area was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Wash.). Mid-day water potential was also measured at approximately solar noon using a pressure chamber (Model 600, PMS Instruments, Corvallis, Ore., USA). Two or three sample shoots were selected from the unshaded portion of treatment branches and at similar branch locations on control branches. At the Wind River sites, predawn water potentials were measured on five understory trees and then corrected for gravitational differences between the understory and the branch pairs (0.01 MPa per meter above ground surface). In these stands, understory trees have been shown to have similar water potentials as canopy trees after accounting for gravitational differences (Bauerle et al. 1999). At the EPA campus, predawn water potentials were measured directly on the experimental branches.

Sap flux on branches in the 10- and 20-year-old trees was monitored using the heat balance technique (Dynagage Model SGA13, Dynamax, Houston, Tex., USA) and in the 450-year-old stand using the heat dissipation technique (Granier 1987). In the 10- and 20-year-old trees, Dynagage sensors were installed prior to the pretreatment diurnal measurements. The gauges were well insulated with both the manufacturer's insulation and with additional reflective insulating foam. Aluminum shields protected both stems and insulated gauges from direct solar radiation. In the 450-year-old tree, 10 mm heat dissipation probes (Granier sensors) were installed in old branches approximately 10 cm in diameter. One sensor was inserted in each experimental branch. Each sensor was supplied with 100 mW power. Branches were insulated with foam pipe insulation and reflective covering to cover ca. 25 cm both upstream and downstream from the Granier sensor pair. Acid-free silicon sealant was applied to the top and along seams where water could enter. Sensors were installed in early spring and monitored throughout the year, but we are presenting only the data during the shading experiment.

The nature of the hydraulic connection between a main branch and lateral branches was examined with young Douglas-fir branches. Conductance of stem segments was measured by applying a known partial vacuum (20–30 kPa) to the base of the segment and flow was measured with calibrated pipettes sealed to the open tip in the segment being measured. The solution in the system was de-gassed water with 20 mM KCl. The hydraulic conductance per unit length [m^4 MPa^{-1} s^{-1}; (Schulte 1993)] was calculated for each measured segment for use in subsequent calculations of a predicted flow increase following branch removal.

Five study branches were measured, each containing a junction with two lateral branches (B and C, Fig. 1a) forking from the main branch (A). First, conductance was measured on the entire section with flow rate being measured at the tips of B and C (ABC). Then, section C was removed and the cut surface was sealed with a clear acrylic copolymer. Conductance was measured again through A and B and flow measured at the tip of B (AB). Finally, A and B were cut apart and conductance was measured on each separate segment, A, B and C. All segment cuts were made under water.

The measured change in flow through lateral branch B after removal of lateral branch C was expressed as a percent increase over the original flow rate measured when both branches were attached. If the xylem of the lateral branches is fully coupled within the main stem, one can predict how the flow should increase following excision of one lateral branch. The predicted flow rate (J_{pred}) was calculated for the pressure applied (ΔP) as if the removed branch had never been part of the xylem system and the entire main stem is utilized for flow to the remaining branch:

$$J_{pred} = \frac{\Delta P}{R_a + R_b} \tag{1}$$

where R_a and R_b are the resistances (MPa s m^{-3}; inverse conductance) measured for the main stem (A) and the lateral branch (B), respectively. This predicted flow was expressed as a percent increase over the measured flow through the system before the re-
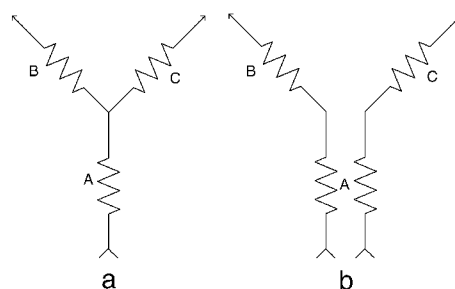

Fig. 1a, b Circuit diagram of the branch junctions used to test hydraulic connectedness. Section A is the main branch, while B and C are forking lateral branches. Two extremes of connectedness are illustrated: **a** where lateral branches are completely interconnected and **b** where lateral branches function as independent units supplied by different section of xylem in main branch A

moval of the competing lateral branch. Since the actual, measured flow was similarly expressed as a percent increase over the initial flow before the removal of the other lateral, then we could compare the predicted and actual flow increases as a way of assessing how interconnected are the xylem elements in the main stem. If no hydraulic interconnection existed (stem xylem is dedicated independently to each branch) then a model like Fig. 1b would be more relevant and severing one lateral would have no effect on flow in the adjacent lateral.

Climate data for the Wind River were provided by Wind River Canopy Crane Research Facility in collaboration with the Western Region of the National Center for Global Ecological Change (http://depts.washington.edu/wrccrf/research.html). The Wind River (WR) data were from a station located in an open field 400 m south of the canopy crane and at the EPA campus, the weather station was located in an open field 50 m west of the measurement trees. Measurements included air temperature (Vaisala HMP35C, Helsinki, Finland at WR and General Eastern 630 MP thermistor Woburn, Mass., USA at EPA), relative humidity (Vaisala HMP35C, Helsinki, Finland at WR and LI COR, LI 6262, Lincoln, Neb., USA, at EPA), and photosynthetic photon flux density (PPFD, LI COR, LI-190).

All statistical analyses were preformed using SYSTAT (Version 9.01, SPSS Science, Chicago, Ill., USA). Treatment or branch differences in diurnal gas-exchange data were tested using repeated measures in a generalized linear model.

Results

Weather during all 6 days of field measurements was typical of late summer in the Pacific Northwest, with relatively dry air, clear skies, and warm temperatures (Table 1). Vapor pressure deficit (D) reached a maximum of 4.46 kPa in the afternoon on 12 September 2001, when the baseline measurements were made on the 10-year-old trees. The following treatment day, 13 September 2001 was similar but was not quite as dry reaching a maximum D of 3.7 kPa. The treatment day for the 20-year-old trees was also relatively dry (D_{max}=4.0 kPa), whereas the other 3 days were not as hot and dry, reaching maximums of 3.0, 2.3 and 2.0 kPa on 24 August, 1 September and 2 September, respectively. PPFD reached a maximum of 1,348–1,374 µmol m^{-2} s^{-1} on all 6 days with some scattered clouds appearing on the 450-year-old stand treatment day (2 September). Maxi-

Fig. 2 Diurnal sapflow patterns on the baseline day (*open symbols*) and the treatment day (*closed symbols*) for four different branches in the 20-year-old stand. *Arrows* indicate the time at which the shading structures were removed from the treatment branches on 26 August 1999
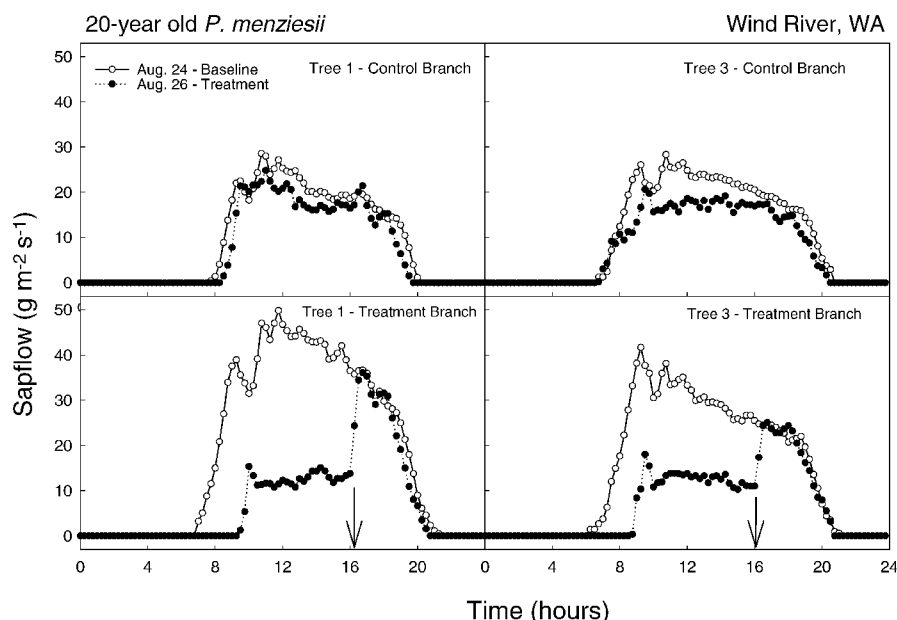

Table 1 Climate data for the six days that measurements were made for this experiment

Date	Stand		T_{max} °C	T_{mean} °C	T_{min} °C	D_{max} (kPa)	PPFD$_{max}$ (mmol m^{-2} s^{-1})
12 September 2001	10-year-old	Baseline	34.3	20.9	10.2	4.46	1,364
13 September 2001	10-year-old	Treatment	32.4	19.6	10.2	3.70	1,374
24 August 1999	20-year-old	Baseline	29.9	21.3	13.2	2.99	1,348
26 August 1999	20-year-old	Treatment	33.2	19.7	8.3	4.01	1,357
1 September 1999	450-year-old	Baseline	24.2	13.3	3.2	1.98	1,356
2 September 1999	450-year-old	Treatment	26.6	15.1	4.7	2.33	1,354

mum temperatures on the measurement days ranged from 34.3°C on 12 September 2001 to 24.2°C on 1 September 1999. Temperatures on the measurement days in the 450-year-old stand were much lower than for the other stands as a small cold front moved through the area on 30 August 1999 with a trace of precipitation.

Sap flux measured before treatments were installed and on control branches after treatments were installed followed a typical pattern for late summer in the Pacific Northwest in the 20-year-old stand (Fig. 2). Measurable sap flux began between 0600 and 0800 hours with the highest rates of sap flux measured early to mid-morning, with a gradual reduction through the day following the increase in D in the afternoon. Branches on the 10-year-old and 450-year-old followed similar patterns with slight variations due to solar radiation reaching the branches and D on the measurement day (data not shown).

Reducing the transpiring leaf area on a branch by shading had the expected effect of reducing transpiration at the branch level (Fig. 2). Transpiration was reduced between 55 and 95% on the treatment branches relative to the baseline measurements in all three sets of *P. menziesii*. It is interesting to note that sap flux within the treatment branches began several hours after sap flux be-

gan in the control branches (Fig. 2). Once the shading was removed after the diurnal gas-exchange measurements were completed, transpiration increased rapidly to values similar to those observed on the baseline day.

Diurnal patterns of gas exchange for all three sets of trees where typical for late summer with the highest photosynthetic rates and g_s values occurring in the morning, followed by a rapid decline in both. For example, in the 10-year old *P. menziesii* trees, maximum g_s was measured before 0800 hours and ranged between 0.04 and 0.08 mol m^{-2} s^{-1} and maximum photosynthesis at light saturation (A_{sat}) ranged between 4 and 8 μmol m^{-2} s^{-1} (Fig. 3, Table 2). g_s decreased until mid-day, then remained between 0.01 and 0.04 mol m^{-2} s^{-1} for the rest of the afternoon (Fig. 3). A_{sat} stabilized slightly later in the day at values roughly one-third of the maximum measured in the morning. The measurements of g_s and A_{sat} in the 10-year-old trees were lower than those measured at the Wind River sites for the 20- and 450-year old trees (Table 2) probably due to the dry air conditions at the EPA site (Table 1). Soil water conditions as indicated by predawn water potential were similar between the sites (measured near ground level), so the 450-year-old tree had the lower leaf water potentials predawn due to gravi-

Table 2 Morning maximum rates of photosynthesis at light saturation and stomatal conductance for both the baseline day and the treatment day for all three stands

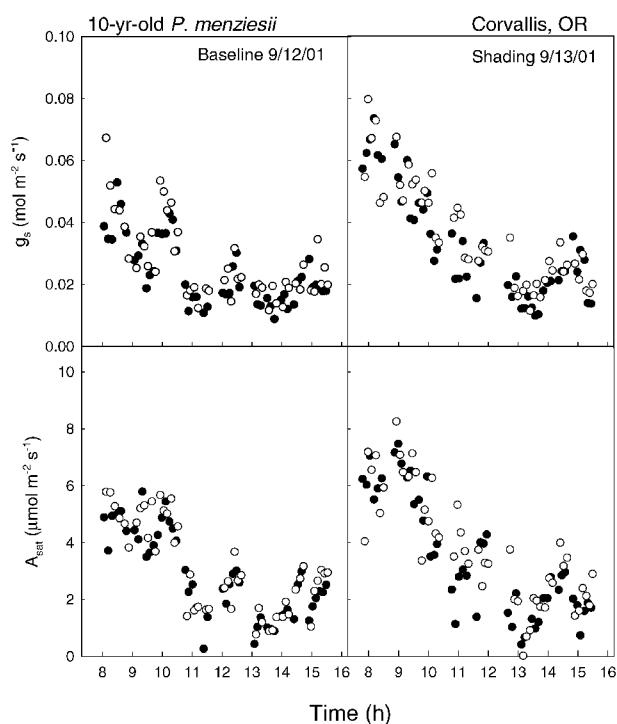| Stand	A_{max} (μmol m^{-2} s^{-1})		$g_{s\ max}$ (mol m^{-2} s^{-1})	
	Control	Shaded	Control	Shaded
10-year-old				
Baseline	4.9±0.61	4.6±0.71	0.039±0.012	0.034±0.010
Treatment	6.5±1.09	6.4±0.65	0.058±0.011	0.058±0.010
20-year-old				
Baseline	11.2±0.1	8.5±0.6	0.19±0.058	0.09±0.013
Treatment	13.2±1.8	10.3±2.2	0.20±0.028	0.15±0.027
450-year-old				
Baseline	9.0±1.1	9.4±1.7	0.16 ±0.025	0.17±0.053
Treatment	7.9±0.4	10.13±1.3	0.19±0.071	0.19±0.081

Fig. 3 Diurnal pattern of gas exchange on the baseline day and the treatment day in September 2001. *Filled symbols* are sunlit foliage samples on the branch selected for shading treatment, *open symbols* are sunlit foliage on the control branches

Fig. 4 A comparison of stomatal conductance of foliage on the control branch with stomatal conductance of sunlight foliage on the treatment branch for both the baseline and the treatment day. Samples were paired by time of day. The line is a 1:1 line

tational effects (Table 3). The decrease in shoot water potential during the day followed a trend similar to g_s (data not shown). The 20-year-old and 450-year-old trees reached much lower mid-day water potentials and had higher g_s than the 10-year-old trees (Tables 2, 3, Fig. 4).

Shading did not appear to have an impact on either g_s, photosynthesis or mid-day water potentials (Fig. 3, Tables 2, 3). For shaded branches, we hypothesized that g_s of the remaining sunlit foliage would increase when competition for water with other transpiring foliage on the branch was reduced or eliminated. However, both sunlit foliage on shaded branches and control branches
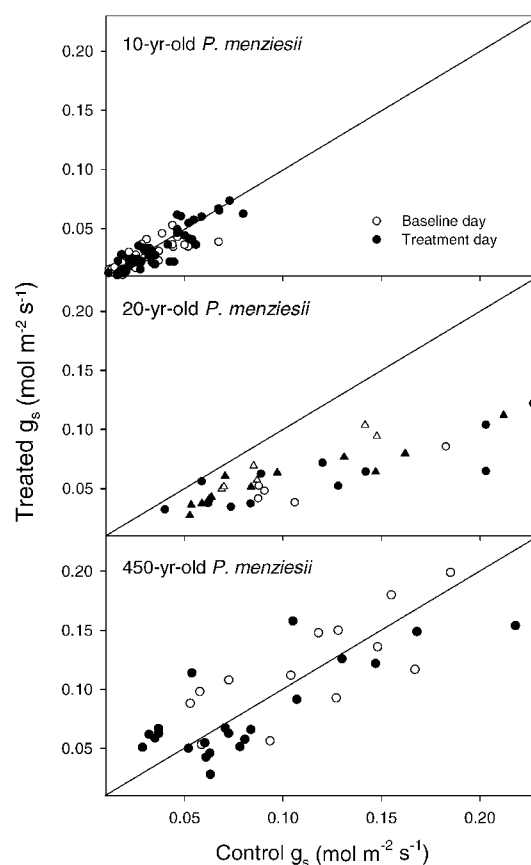
behaved similarly throughout the day (Fig. 3). When control foliage g_s was compared to treatment foliage g_s, the differences between the foliage samples were the same for the baseline and the treatment day (Fig. 4). For the 20-year-old trees, g_s was slightly lower in the treatment foliage compared to the control foliage for both measurement days, so the points fall below the one to

Table 3 Mid-day and predawn water potentials in MPa (± SD) for both the baseline and treatment days at both sites. Mid-day water potentials were measured between noon and 3 pm. Predawn water potentials at the Wind River Stands were measured on understory trees, which have been show to have similar water potential values as canopy trees after accounting for gravitational differences (Bauerle et al. 1999)

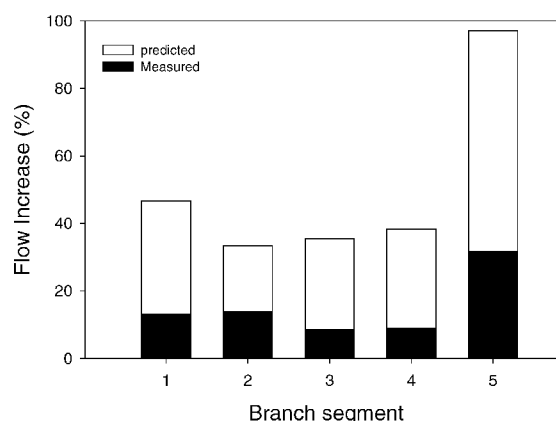| 10-year-old stand		20-year-old stand		450-year-old stand	
Baseline (12 September 2001)		Baseline (24 August 1999)		Baseline (1 September 1999)	
Control branch	−1.6±0.15	Control branch	−2.2±0.15	Control branch	−2.4±0.04
Covered branch	−1.6±0.20	Covered branch	−2.3±0.27	Covered branch	−2.4±0.10
Shading (13 September 2001)		Shading (26 August 1999)		Shading (2 September 1999)	
Control branch	−1.6±0.19	Control branch	−2.0±0.13	Control branch	−2.3±0.18
Covered branch	−1.6±0.24	Covered branch	−1.9±0.14	Covered branch	−2.4±0.16
Predawn	−0.6±0.04	Predawn[a]	−0.85±0.05	Predawn[a]	−1.05±0.21

[a] Values have been gravity corrected
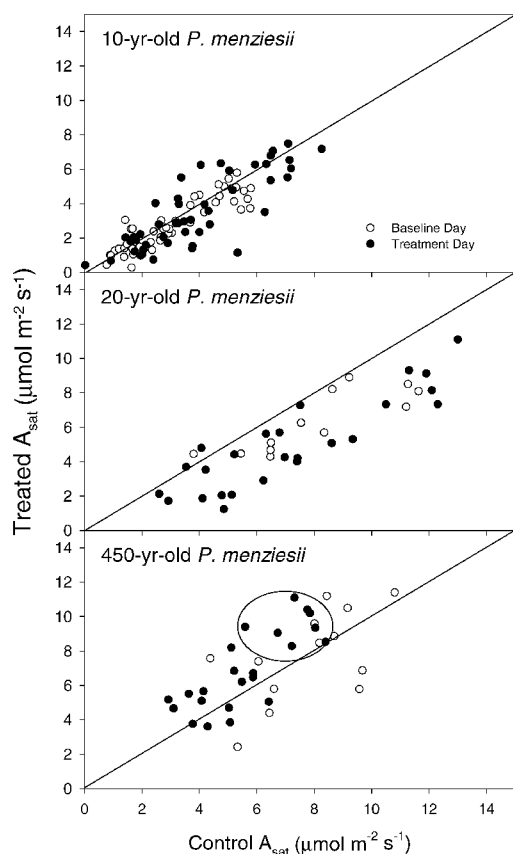
Fig. 5 A comparison of photosynthesis at light saturation of foliage on the control branch with photosynthesis at light saturation of sunlight foliage on the treatment branch for both the baseline and the treatment day. Samples were paired by time of day. The line is a 1:1 line

Fig. 6 The percent increase in flow to a lateral branch when flow to competing laterals has been stopped. The predicted increase in flow represents the increase expected if xylem was completely coupled. *Branch segment* are the replicates (1–5) from five different branches on different trees

one line; however, the points for treatment day fall along the same line as those for the baseline. For all age-classes of trees, no significant difference was observed between the two days ($P > 0.1$ for all three, Fig. 4). This lack of difference between treatment and control branches was also found in the mid-day water potential measurements (Table 1).

For photosynthesis, shading had no effect on the 10- or 20-year old trees (Table 2, Fig. 5). However, on the treatment day for the 450-year-old trees, A_{sat} was significantly greater in the morning on the treatment branch relative to the control ($P = 0.021$, circled points on Fig. 5), where photosynthesis on the treatment branch averaged 10.1 µmol m^{-2} s^{-1}, compared to 7.9 µmol m^{-2} s^{-1} on the control branch (Table 2). This difference in A_{sat} was not reflected in either g_s ($P = 0.945$) or water potential measurements (Fig. 4, Table 3). Maximum g_s averaged 0.19 mol m^{-2} s^{-1} for both treatment and control samples on the treatment day (Table 2). Mid-day water potentials were approximately −2.4 MPa for both control and treatment branches for both baseline and treatment days (Table 3).

After the shading experiment, we measured the hydraulic conductance of branch junctions to determine whether reduced flow to one part of a branch could increase flow to another. Flow through a lateral branch increased an average of 15% once a competing lateral was removed (ranging between 9% and 31%, Fig. 6). The variance between the five branch segments was

related to the relative difference in diameter of the removed lateral compared to the remaining lateral. If the xylem of these segments had been completely interconnected, the flow increase should have been higher, with an average of a 50% increase rather than 15%. For the five segments we tested, the actual increase in flow was 30% of what we predicted if the hydraulic systems within shoots were completely interconnected.

Discussion

At the branch level, shading to reduce the amount of transpiring foliage did not affect g_s of the remaining sunlit foliage. In addition, photosynthetic rates in the remaining sunlit foliage were also unchanged by branch-level shading with the exception of one tree. Since neither g_s nor water potential changed for that treatment branch in response to shading, we speculated that the shading structure (white plastic covered with aluminum foil) may have backlit the remaining sunlit foliage which fully activated the photosynthetic machinery within those shoots (note: all measurements were made under constant light conditions). The fact that g_s did not also respond to the higher rates of photosynthesis further supports our conclusion that branch-level shading did not change the water status of the remaining sunlit shoots.

There are a number of possible reasons why branch level shading failed to affect g_s of the remaining sunlit foliage on the branch, and they relate to how water moves along the entire pathway from the soil to the leaf. It appears that for g_s to change in response to hydraulic alterations of the pathway, issues of scale and total pathway resistance are important. Shading of foliage would increase g_s of sunlit foliage if shading part of the foliage on the branch increased the "effective" leaf specific conductance for remaining foliage. Meinzer and Grantz (1990) proposed that the ratio of transpiring leaf area to hydraulic conductance regulates g_s, and on a whole-tree level this appears to be true. Whitehead et al. (1996) shaded 78% of a tree's foliage, albeit in the lower crown, and significantly lowered total canopy transpiration when they observed a significant increase in g_s in the remaining sunlit foliage. However, when Whitehead et al. (1996) shaded the upper 22% of their *Pinus radiata* canopy, they did not see a similar increase in g_s in the lower 78% of the canopy the way they did when they shaded the lower part of the canopy. Pepin et al. (2002) shaded 50% or more of the lower foliage on *Thuja plicata* seedlings, which lowered total canopy transpiration, but by less than the proportion of leaf area that was shaded and increased g_s by approximately 10–20% on the remaining sunlit foliage. The degree of response seemed to be related to the reduction in canopy transpiration. They did not lower the amount of shaded foliage to see if there were a threshold of shading to induce a change in g_s. The hydraulic system at the whole tree level appears to be interconnected well enough that when transpiration of the tree is reduced, upper canopy sunlit foliage can increase g_s.

At the branch level, our data support the alternative that hydraulic systems within a branch are relatively unconnected. We shaded between 85% and 90% of the foliage on an individual branch and observed no significant changes in stomatal behavior of the remaining sunlit foliage, even though branch transpiration was reduced by 65–90%. As we expected, our small amount of shading did not change total tree transpiration (N. Phillips, unpublished data). Pataki et al.(1998) found an increase in whole canopy conductance with a leaf area removal treatment, but did not find similar g_s changes with leaf-level measurements. In addition, Phillips et al. (2001) also found that g_s was relatively insensitive to branch leaf-area removal in two tropical tree species. In contrast to these results, Hubbard et al. (1999) did find a significant increase in g_s early in the growing season in foliage on branches of older *Pinus ponderosa* after 50% of the leaf area had been removed from the branch. However, this response was not found in younger trees, nor was it detected later in the growing season in the same branches on older trees. Hubbard et al. (1999) speculated that the lack of late season response could be that new foliage production increased branch leaf area and negated the effect of the earlier foliage removal. It appears that in most cases, altering the ratio of transpiring leaf area to hydraulic conductance at the branch level has no effect on g_s.

We also have direct evidence that shoots on a branch have limited hydraulic interconnection (Fig. 6). When we examined how well coupled the xylem was between lateral branches diverging from the main stem on a branch, we found the measured increase in flow through the remaining lateral branch was considerably less than predicted for complete coupling. This difference suggests that a model of the branch junction as a simple y-shaped network of resistances (Fig. 1a) is inadequate because the stem xylem is not fully coupled. After excision of one branch, the remaining branch is not capable of fully utilizing all of the xylem in the stem below the junction. Thus, xylem connections partially isolate shoots so they could be autonomous to some extent to changes in transpiration in the rest of the branch (Shinozaki et al. 1964a; Sprugel et al. 1991). Most models of water transport use the basic Ohms law analogy for water movement within the xylem, and those models would predict complete interconnection between shoots (Fig. 1a). For circuit models using Ohms law analogy connecting all leaves and branches to common source, variation in flow to the competing sinks is driven simply by pathway resistance and the driving gradient (Tyree and Ewers 1991). The other extreme is the pipe model where each unit of foliage is supplied by a separate and independent pipe (Fig. 1b) (Shinozaki et al. 1964a, 1964b). In this case, water in one pipe is not available to a competing sink. Our results indicate that in *P. menziesii* the actual connection between shoots on a branch is somewhere in between. If branches on a tree behave in a similar manner to the lateral shoots on these branches, then branches may have partially autonomous behavior in terms of water. Sprugel et al. (1991) stated that a branch, or in this case a shoot, could be considered autonomous

with respect to water if it is insulated from factors that affect other branches. Perhaps this partial autonomy could help explain why stomatal responses on the whole tree level occur when more than 50% of the foliage is shaded, but not when 22% was shaded (Whitehead et al. 1996; Pepin et al. 2002). In the Hubbard et al. (1999) study where they did see an increase in g_s, they removed 50% of the foliage by removing every other needle, so the treatment was equally distributed among all the shoots, and shoot isolation would play less of a role on the stomatal response.

The lack of stomatal response to these shading treatments implies that when a branch is in partial shade, the remaining sunlit foliage on that branch has no advantage with water status over foliage on a branch completely in the sun. This does suggest that there is some degree of autonomy and isolation of xylem pathways, and that transient shading within the canopy may not improve water status of the remaining sunlit foliage until a substantial portion of the canopy becomes shaded as observed by Whitehead et al. (1996) and Pepin et al. (2002).

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